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THE GYMNOSPERMS OF MOUNT KINABALU

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INTRODUCTION

Mount Kinabalu, in the Malaysian state of Sabah in northern Borneo, is the highest mountain in Borneo and between the Himalayas and New Guinea. It encompasses an area of about 700 km^2, and ranges in elevation from slightly above sea level to a maximum height of 4101 m on Low's Peak. Geologically, Kinabalu is one of the most recent major massifs in the world. It is an adamellite (granitic) pluton, which has been uplifted diapirically in the last 1.5 million years and may still be rising at a rate of about 0.3 cm/year. During the Pleistocene the summit supported an ice cap 5 km^2 in extent. Deglaciation of the summit occurred about 9,200 years ago. Moraines have been observed as low as about 3,000 m (Jacobson 1978; Myers 1978).

Kinabalu is thought to have one of the richest floras in the world for a local area (Beaman & Beaman 1990), with more than 4,000 species of vascular plants. Over 180 families and 950 genera occur in the flora. The high species diversity apparently results from a combination of factors, among which the most important are: 1) great altitudinal and climatic range from tropical rain forests near sea level to freezing alpine conditions at the summit; 2) precipitous topography causing effective geographic and reproductive isolation of species over short distances; 3) geological history of the Malay Archipelago; 4) a diverse geology with many localized edaphic conditions, particularly serpentine or ultramafic substrates; and 5) frequent climatic oscillations influenced by El Niño events.

While preparing a botanical inventory of all vascular plants on Mount Kinabalu, we have accumulated data on the gymnosperms that are ready to publish, hence this report. Accounts of the pteridophytes (Parris et al. 1992) and the orchids (Wood et al. 1993) have already been published. Those studies recognized 620 pteridophyte and 711 orchid taxa. The remaining monocot and dicot families are not yet ready for publication. The Kinabalu gymnosperms have not previously been the subject of an independent publication, notwithstanding that some of them are dominants or subdominants in the high-elevation vegetation. Furthermore, certain species have economic value as timber trees, although their limited occurrence on Kinabalu is mostly protected within Kinabalu Park.

The enumeration that forms the body of this paper includes three families of Coniferales, namely Araucariaceae, Phyllocladaceae, and Podocarpaceae and the Gnetaceae (Gnetales). Nine genera are recognized; the number of species and additional infraspecific taxa are indicated in parentheses as follows. Araucariaceae:

Agathis (3); Phyllocladaceae: *Phyllocladus* (1); Podocarpaceae: *Dacrycarpus* (2); *Dacrydium* (5); *Falcatifolium* (1); *Nageia* (1); *Podocarpus* (6); *Sundacarpus* (1); Gnetaceae: *Gnetum* (6; 2). Thus, 26 species of gymnosperms, and two additional varieties, are currently recognized in the Kinabalu flora. The occurrence of 28 gymnosperm taxa in the limited area of Mount Kinabalu would seem to indicate that they represent a rather diverse component in terms of world-wide gymnosperm diversity, but we lack data for comparable areas.

HISTORICAL ASPECTS

The first account of Kinabalu gymnosperms was by Stapf (1894) in his scholarly treatise, "On the Flora of Mount Kinabalu, in North Borneo." He listed five species, only four of which were fully determined. Two of the species Stapf treated had names in approximate agreement with those in the present account. Twenty years later Stapf (1914) reported seven gymnosperms, based on the materials in his previous study with the addition of the 1910 collections by Lilian S. Gibbs.

Subsequent to the reports by Stapf, Meijer (1965a) mentioned nine taxa, including the genera *Gnetum*, *Phyllocladus*, *Podocarpus*, *Dacrydium*, and *Agathis*. Most of these were also illustrated by him (Meijer 1965b). Corner (1978) listed 13 species of conifers, but one of these (*Podocarpus glaucus*) is not presently considered to occur in Borneo and another (*Podocarpus polystachyus*) is a strictly coastal species. Cockburn (1980), although not attempting to list the gymnosperms of Kinabalu, included 12 species that occur on the mountain and illustrated most of them.

The two most important publications relating to the taxonomy of the gymnosperms of Mount Kinabalu are the *Flora Malesiana* treatments of *Gnetum* (Markgraf 1951) and of the Coniferales (de Laubenfels 1988). The present account follows those treatments in generic and species concepts, but some varieties of *Gnetum* proposed by Markgraf are not recognized. Not all taxonomists would accept the generic concepts of de Laubenfels for segregates of *Podocarpus* and *Dacrydium*, nor his species distinctions in *Agathis*, but during this study they appeared to be useful distinctions that are followed here.

COLLECTIONS OF KINABALU GYMNOSPERMS

Up to 1931 only about 26 specimens of gymnosperm had been collected on the mountain, four by H. Low in 1851 or 1858, five by G. D. Haviland in 1892, 11 by L. S. Gibbs in 1910, and 6 by M. S. Clemens in 1915. In 1931–33 J. and M. S. Clemens collected intensively on the south and west sides of the mountain, probably obtaining over 9000 numbered collections plus many others that they did not number. Our records include 106 of their gymnosperm collections from that period. Other significant collections of gymnosperms have been obtained by the Royal Society expeditions in 1961 (Chew, Corner & Stainton) and 1964 (Chew & Corner) (32 numbers), by W. Meijer (23 numbers) in 1959–1963, by S. Kokawa and M. Hotta (21 numbers) in January–February, 1969, by P. F. Cockburn and Aban Gibot (17 numbers) in 1976, by D. J. de Laubenfels (the only taxonomist specializing in gymnosperms ever to have collected on the mountain; 43 numbers) in August, 1978, and January, 1979, and by the Beaman team (29 numbers) in 1983–84 and 1992. Even now the Kinabalu gymnosperms could hardly be said to be well

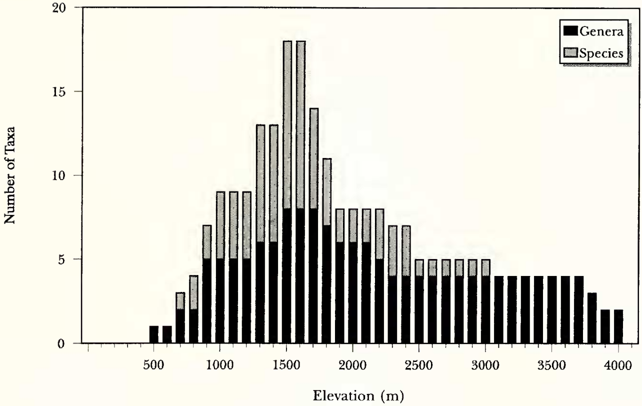

FIG. 1. Elevational distribution of gymnosperms on Mount Kinabalu.

collected; the present study is based on about 446 collections and 700 specimens obtained by 74 collectors or collecting teams.

ECOLOGICAL CONSIDERATIONS

Gymnosperms are scattered in the Kinabalu vegetation from the lowest to highest elevations. They are ecological dominants just below the summit area. Kitayama (1991) recognized 'Tropical lower-subalpine coniferous forest' and 'Tropical upper-subalpine forest'; the dominant species include the gymnosperms *Phyllocladus hypophyllus* and *Dacrycarpus kinabaluensis*, along with the angiosperm trees (or shrubs) *Leptospermum recurvum*, *Eugenia (Syzygium) kinabaluensis*, *Rhododendron buxifolium*, and *Schima brevifolia*. In addition to these two important gymnosperms in the summit flora, Fig. 1 shows that two other species (*Podocarpus brevifolius* and *Dacrydium gibbsiae*) also extend to high elevations.

In spite of the relative importance of gymnosperms in the high-elevation vegetation of Kinabalu, maximum gymnosperm generic and specific diversity occurs at about 1500 m (Fig. 1), a circumstance that also pertains to the pteridophytes (Parris et al. 1992) and orchids (Wood et al. 1993). Corner (1978) noted that *Agathis* was a common big tree from the Mesilau River across the Pinosuk Plateau. Much of that area is at an elevation of about 1500 m. The natural vegetation of the Pinosuk Plateau, formerly part of Kinabalu Park, has been virtually destroyed by various development projects in the past 10 years. Ironically, some spindly pines (*Pinus*) have been planted on the Pinosuk Plateau golf course, probably in almost the exact spot where magnificent *Agathis* trees once stood. *Agathis* was also common in the lower-elevation hill forest on the ultramafic Hempuen Hill, but after that area was degazetted from the Park in 1984, it became a virtual free-for-all for various land grabs, logging, and unsuccessful slash-and-burn agriculture. Most of that forest spared from such activities was consumed by forest fires in 1990.

The species of *Gnetum* are all lianas, often large and extending high into tree crowns in the lowlands, hill forest, and lower montane forest. *Gnetum latifolium* var. *minus* extends up to 1800 m at Tinekuk Falls and *G. leptostachyum* var. *abbreviatum* to the same elevation in the Kilembun basin and at Marai Parai, if Clemens elevation data are to be believed. The rare species *G. gnemonoides* (from the east side of Kinabalu), with huge seeds, and *G. klossii* (from the west side) are known only from lowlands and hill forest, respectively. *Gnetum cuspidatum* and *G. neglectum* are not readily distinguishable from the relatively common *G. leptostachyum* var. *leptostachyum*, which occurs in hill forest and lower montane forest at a number of localities.

Possibly the most abundantly collected of all species in the Kinabalu flora is *Phyllocladus hypophyllus*, now known from 60 collections and 91 specimens. As noted by Corner (1978), it is an Australasian element and extends from Borneo to Sulawesi, Maluku, the Philippines, and New Guinea; other species are known from New Zealand and Tasmania. Keng (1974) considered *Phyllocladus hypophyllus* to be the most primitive living gymnosperm. We have seen large trees of it on the Pinosuk Plateau, but at the highest elevations it is reduced to a low shrub or treelet.

Dacrycarpus imbricatus var. *patulus* and *D. kinabaluensis* are related taxa that were originally treated as the same species; however, they seem readily distinguishable and occur exclusively at different elevations. *Dacrycarpus imbricatus* var. *patulus* is a species of lower montane forest, hardly occurring above 2000 m. *Dacrycarpus kinabaluensis*, on the other hand, is a strictly high-elevation species of upper montane forest and summit scrub, which rarely occurs below 2500 m. De Laubenfels (1988) noted that on Kinabalu *D. imbricatus* does not occur above 2000 m, and indeed the high-elevation figure we have is based on the specimen *Clemens 33618* from the Penataran basin and may be erroneous. *Dacrycarpus imbricatus* is widely distributed in Borneo, Southeast Asia, the Malay Peninsula, Sumatra, Mindanao, Sulawesi, New Guinea, the New Hebrides, and Fiji, whereas *D. kinabaluensis* is endemic to Mount Kinabalu.

One of the most distinctive trees in the upper montane forest is *Dacrydium gibbsiae*, conspicuous along the summit trail from about 2500 m to 3000 m. The species is a very graceful plant of ‘Christmas tree’ aspect with drooping lower branches. It appears to be restricted to ultramafic substrates, such as those in the area of mossy forest on ridges between Layang-layang and Paka-paka Cave. Found just below this area, in a zone from about 2000 to 2500 m, is *Dacrydium xanthandrum*, readily distinguishable because its leaves are slightly longer than those of *D. gibbsiae*, and extend perpendicular to the stem rather than curving stiffly upward and inward as in *D. gibbsiae*.

Along the road from Park Headquarters to the Power Station, in the elevation range of 1500 to 1800 m, several gymnosperms can be seen, including *Agathis kinabaluensis*, *A. lenticulata*, *Dacrycarpus imbricatus* var. *patulus*, *Dacrydium gracilis*, *Falcatifolium falciforme*, *Podocarpus laubenfelsii*, and *Sundacarpus amara*. In this area Cockburn performed a useful service by collecting lower, middle, and upper branches from trees of several different species. Through these collections one can better understand the extent of foliage variation on individual trees and thus better interpret specimens for which the collector did not indicate the part of the tree from which they were obtained.

Eight of the Kinabalu gymnosperms (i.e., about one-third of the taxa) are found predominantly or entirely on ultramafic substrates. These are: *Agathis borneensis*, *Gnetum leptostachyum* var. *abbreviatum*, *Dacrydium gibbsiae*, *D. pectinatum*, *Podocarpus brevifolius*, *P. confertus*, *P. gibbsii*, and *P. globulus*. Ultramafic substrates are extremely important in the occurrence of orchids on Kinabalu (Wood et al. 1993), but proportionally fewer of the gymnosperms seem restricted to ultramafic substrates.

The following six taxa are thought to be endemic to Mount Kinabalu: *Agathis kinabaluensis*, *Gnetum leptostachyum* var. *abbreviatum*, *Dacrycarpus kinabaluensis*, *Dacrydium gibbsiae*, *Podocarpus brevifolius*, and *P. gibbsii*. Five others, i.e., *Dacrydium gracilis*, *Podocarpus confertus*, *P. globulus*, *P. laubenfelsii*, and *Agathis lenticulatus*, are endemic to Borneo. The other species are largely centered in the Malesian region, particularly Borneo; *Phyllocladus hypophyllus* is the conspicuous Australasian element.

METHODS

The overall concept of the botanical inventory of Mount Kinabalu as a taxonomic database was outlined by Beaman and Regalado (1989). An integrated system of computer programs used for data editing and printing the gymnosperm enumeration (as well as those for other parts of the project) was written in the dBASE IV programming language by Reed Beaman. A management program, KINABALU, allows for accessing any aspect of the database through a menu system. Six principal relational data files were employed. Two of these files contain data on specimens including types. Taxonomic, nomenclatural, and bibliographic information is linked from other files. Various procedures permit creating and editing a database. Menus facilitate inputting and editing specimen and taxon data, globally replacing various expressions such as changing an author's name or abbreviation, indexing and querying the database, computing a summary of elevation ranges for taxa, numbering taxa, making an index to numbered collections, and printing enumerations of all taxa in the database or selected families or genera.

One objective of the project has been to examine critically all specimens upon which the Enumeration is based. For the gymnosperms, these include approximately 700 specimens located in six herbaria: BM, K, L, MSC, SING, and SNP (Sabah Parks Herbarium on Mount Kinabalu). From an examination of specimen citations it can be seen that certain species have been very much collected on the mountain and others very little. In the case of the rather conspicuous gymnosperms, the number of specimens cited probably is a fairly good indicator of the frequency of that taxon on the mountain.

For purposes of brevity, and especially to facilitate effective queries of the database, we have used standardized locality data in the Enumeration. A list of the standardized locality names, with their geographic coordinates, is provided by Beaman et al. (in press). It may be noted that some locality names are rather different from those on specimens and in the literature, because we have attempted to use spellings established in accordance with the modern Dusun language.

Elevation data are summarized for all taxa for which these data were available on specimen labels. The elevation range indicated for taxa is based on the lowest and highest elevations recorded (whether in feet or meters) for specimens of each taxon and rounded to the nearest 100 m. In some taxa certain specimens have no elevation data while others do. It may be apparent from the locality data that a particular taxon must occur at lower or higher elevations than indicated by the elevation recorded. We have refrained from providing elevation ranges for taxa when the specimens do not provide this information, with the result that the elevations stated are sometimes misleading or incorrect.

Taxonomic treatments that the Enumeration follows are indicated at the beginning of each family and genus. Type specimens are cited only for taxa described from Mount Kinabalu. The synonymy includes only names based on types from Kinabalu. Names of authors of taxa are abbreviated in accordance with the standardized list of author abbreviations (Brummitt & Powell 1992).

In order to produce an index of determined specimens, it is necessary to have the taxa numbered. In the treatment of pteridophytes for the Kinabalu inventory, 30 families were recognized and numbered in alphabetical order. The gymnosperms start with family 31 and likewise are numbered in alphabetical order, except that the Gnetaceae are placed after the conifers as family 34. Therefore, the numbering of the gymnosperms begins with the Araucariaceae as family 31 and goes on to the other families. Within each family the genera are alphabetically numbered and likewise species within genera. Nominate subspecies or varieties always precede other infraspecific taxa, regardless of alphabetical order.

TAXONOMIC PROBLEMS

The enumeration of *Gnetum* presented here may not be very sound. Markgraf's treatment in *Flora Malesiana* was based largely on his earlier (1930) monograph. At the time of that work hardly any specimens of *Gnetum* from Kinabalu had been collected. Relatively few of the specimens we examined have his annotations. *Gnetum* is particularly difficult because some of the best characters are in the seeds and the branches on which they are borne. Since the plants are dioecious, a rather high percentage of specimens lack these reproductive structures. The characters of leaf venation that Markgraf used also are difficult to recognize and probably do not hold up very well. A modern taxonomic account of the genus is much needed.

Agathis is also a difficult genus, and the two higher-elevation species recognized in this account (*A. kinabaluensis*, *A. lenticulata*) may be local ecological variants. On Kinabalu, however, they seem reasonably distinguishable and are therefore retained. An alternative view of *Agathis* is provided by Whitmore (1980), who included material here recognized in *A. kinabaluensis* and in *A. lenticulata* as *A. dammara* (Lamb.) Rich. subsp. *dammara*. According to Whitmore's treatment, *A. dammara* does not occur in Borneo except in some mountainous areas. Whitmore emphasized characters of the male cones and considered leaf shape and size to be highly and continuously variable.

Cockburn (1980) indicated that the splitting of *Podocarpus* into several smaller genera was difficult to condone when even the differences between *Dacrydium* and *Podocarpus* are so fine as to make these genera unworthy of separation. He regarded *Podocarpus imbricatus* (i.e., *Dacrycarpus imbricatus*) as a large, widespread species with a number of ecotypes associated with altitude and exposure in which the proposed varieties merge imperceptibly into one another. We find, however, that *Dacrycarpus kinabaluensis* and *D. imbricatus* are almost always readily distinguishable. Page (1988) noted that the diagnoses of many of these genera often depend heavily on vegetative aspects of the plants, in a group whose reproductive aspects offer a rather limited array of features. He further indicated that most of the small genera in the Podocarpaceae are fairly natural groupings with good geographic and probably evolutionary cohesion, supported in many cases by cytological and phytochemical data.

Because of the utility of vegetative characters in distinguishing many of the taxa, we have included a vegetative key to genera and have provided figures for all the taxa, which mostly represent vegetative characters. We hope the emphasis of such features will facilitate identification, because many specimens are collected in sterile condition.

A few specimens of *Podocarpus* are tentatively determined. One of these is *Beaman 10362* from Mamut Copper Mine. This collection lacks the distinctively erect disposition of the leaves, characteristic of *Podocarpus brevifolius*, and occurs at a lower elevation than normal for the species. However, it seems to be more in accord with that taxon than any other currently recognized species.

The juvenile material, or perhaps lower branches, that collectors have obtained of certain species sometimes makes identification difficult. For example, in the mature state and from upper branches, *Dacrydium gibbsiae* and *D. gracilis* are highly distinctive, but young individuals or lower branches can have a different aspect with much longer and more similar leaves.

VEGETATIVE KEY TO THE GENERA OF GYMNOSPERMS ON MOUNT KINABALU

1. Large woody climbers. Leaves opposite, of dicotyledonous aspect. *Gnetum.*
1. Trees, or, at high elevations, shrubs. Leaves or phyllodes opposite or alternate, more or less scleromorphic.
  2. True leaves absent, these replaced by cladodes or flattened shoots. *Phyllocladus.*
  2. Leaves present, needlelike, scalelike, or expanded into broad blades.
    3. Leaves opposite, the largest more than 2 cm wide.
      4. Terminal buds globose. *Agathis.*
      4. Terminal buds acute. *Nageia.*
    3. Leaves spirally arranged, less than 2 cm wide.
      5. Leaves, at least some of them, more than 3 cm long.
        6. Principal leaves bilaterally flattened, falcate. *Falcatifolium.*
        6. Principal leaves with distinct upper and lower surface.
          7. Midvein on the upper surface with a longitudinal groove. *Sundacarpus.*
          7. Midvein not grooved. *Podocarpus.*
      5. Leaves all relatively small, needlelike or scalelike, less than 3 cm long.
        8. Foliage dimorphic. *Dacrycarpus.*
        8. Foliage not dimorphic, needlelike. *Dacrydium.*

ENUMERATION OF TAXA

Kramer, K. U., & Green, P. S., eds. The Families and Genera of Vascular Plants. Kubitzki, K., ed. I. Pteridophytes and Gymnosperms. Springer-Verlag, Berlin etc.; Gymnosperms, pp. 279–391. 1990.

31. ARAUCARIACEAE

De Laubenfels, D. J. Araucariaceae. Fl. Males. I, 10: 419–442. 1988.

31.1. Agathis

De Laubenfels, D. J. *Agathis*. Fl. Males. I, 10: 429–442. 1988. De Laubenfels, D. J. The species of *Agathis* (Araucariaceae) of Borneo. Blumea 25: 531–541. 1979.

31.1.1. Agathis borneensis Warb., Monsunia 1: 184. 1900. Fig. 2.

Large tree. Hill forest, sometimes on ultramafic substrate. Elevation: 800–1400 m.

Specimens Examined. Dallas: 900 m, *Clemens 27302* (BM); Hempuen Hill: 800–1000 m, *Beaman 7425* (MSC), 800–1200 m, *7694* (K, MSC), 1400 m, *Beaman et al. SNP 5068* (SNP); Mt. Nungkek: 900–1200 m, *Clemens 32821* (BM, L).

31.1.2. Agathis kinabaluensis de Laub., Blumea 25: 535. 1979.—Type: Summit Trail, 2000 m, *de Laubenfels P 625* (holotype: L!). Fig. 3.

Small to large tree. Lower montane forest, sometimes in mossy forest on ridges. Elevation: 1500–2200 m. Endemic to Mount Kinabalu.

Additional Specimens Examined. Bambangan River: 1500 m, *RSNB 4457* (K, SING); Eastern Shoulder: *Phillipps SNP 2165* (SNP); Kiau: *Clemens 10004* (BM, K); Kiau View Trail: 1600 m, *Beaman et al. SNP 5077* (SNP), 1600 m, *Justine SNP 675* (SNP), 1600 m, *SNP 767* (SNP); Kilembun Basin: 1700 m, *Clemens 34496* (BM, K, L); Mempening Trail: 1700 m, *de Laubenfels P 646* (L); Mesilau Cave: 1900–2200 m, *Beaman 9556* (K, MSC), 1800 m, *RSNB 4778* (K, SING); Mt. Tembuyuken: *Nais et al. SNP 4826* (SNP); Park Headquarters: 1700 m, *Gimpiton et al. SNP 937* (SNP), 1700 m, *de Laubenfels P 644* (L), 1700 m, *P 720* (L).

31.1.3. Agathis lenticulata de Laub., Blumea 25: 537. 1979.—Type: Park Headquarters, 1500 m, *de Laubenfels P 619* (holotype: L!). Fig. 4.

Large tree. Lower montane forest. Elevation: 900–1800 m.

Additional Specimens Examined. Kilembun Basin: 1700 m, *Clemens 34496* (BM); Liwagu River Trail: 1500 m, *Lajangah SAN 44400* (K, L), 1500 m, *Sadau SAN 42812* (K, L), 1500 m, *de Laubenfels P 637* (L); Mamut Hill: 1500–1800 m, *Kokawa & Hotta 5676* (L); Mesilau River: 1500 m, *RSNB 4249* (K, L, SING), 1500 m, *RSNB 4330* (K, L, SING), 1500 m, *de Laubenfels P 621* (L); Mesilau/Bambangan Rivers: 1600–1700 m, *Kokawa & Hotta 4280* (L); Mount Kinabalu: *Aban SAN 56636* (SNP), 1700 m, *Binideh SAN 65171* (SING), 1600 m, *Dolois & Ansow SNP 1941* (SNP); Park Headquarters: 1400 m, *Abbe et al. 9973* (L), 1600 m, *Beaman & Ansow SNP 5060* (SNP), 1600 m, *Binideh SAN 65143* (K), *SAN 65144* (SNP), 1600 m, *Kokawa & Hotta 6128* (L), 1500 m, *Lowry 649* (L), 1200 m, *Meijer SAN 22111* (K), 1600 m, *Phillipps SNP 1516* (SNP), 1500 m, *de Laubenfels P 620* (L); Penibukan: 1200 m, *Clemens 40732* (BM); Tenompok: 1500 m, *Clemens 28145* (BM), 1500 m, *28390* (BM, K, L), 1500 m, *28729* (BM, K), 1400 m, *Melegrito A 473* (K, L, SING), 1400 m, *Smythies S 10602* (K, L, SING); Tenompok/Ranau: 1500 m, *Carr SFN 27005* (SING).

32. Phyllocladaceae

32.1. Phyllocladus

De Laubenfels, D. J. *Phyllocladus*. Fl. Males. I, 10: 355–360. 1988. De Laubenfels, D. J. A revision of the Malesian and Pacific rainforest conifers, I. Podocarpaceae, in part. J. Arnold Arb. 50: 277–282. 1969. Keng, H. 1978. The genus *Phyllocladus* (Phyllocladaceae). J. Arnold Arb. 59: 249–273.

32.1.1. Phyllocladus hypophyllus Hook. f., Icon. Pl. n.s. 5: t. 889. 1852.—Type: Mount Kinabalu, 2400 m, *Low s.n.* (holotype: K!). Fig. 5.

Large to small tree, shrubby and gnarled at high elevations. Lower montane forest, upper montane forest, mossy forest on ridges, low mossy and xerophyllous scrub. Elevation: 1200–4000 m.

Additional Specimens Examined. Eastern Shoulder: 2300 m, *RSNB 710* (K, L, SING); Gurulau Spur: 2400–2700 m, *Clemens 50626* (BM), *50784* (BM, L), 3000 m, *50797* (BM, L), 3400–3700 m, *51220* (BM); Kemburongoh: 2100 m, *Mikil SAN 56277* (K, L), 2100 m, *Price 183* (K), 2100 m, *Sinclair et al. 9053* (SING), 2200 m, *Smith 453* (L); Kinateki River Head: 2100 m, *Clemens 31838* (L); Kundasang: *Burgess SAN 25167* (K), 1500–1800 m, *Meijer SAN 21968* (K); Layang-layang: 2200 m, *Andrews 883* (K); Lubang: 1800 m, *Gibbs 4152* (BM, K); Mamut Copper Mine: *Aban SAN 66823* (SING); Marai Parai: 1500 m, *Clemens 31927* (K), 1500 m, *32459* (BM, L); Marai Parai Spur: *Clemens 10957* (BM), 2100 m, *Gibbs 4088* (BM, K); Mesilau Basin: 2400–2700 m, *Clemens 29743* (BM, K, L); Mesilau Cave: 1800 m, *RSNB 4824* (K, SING); Mesilau Cave Trail: 1700–1900 m, *Beaman 8000* (MSC); Mesilau River: 1500 m, *RSNB 4172* (K, L, SING); Mesilau Trail: *Chow & Leopold SAN 74513* (K, L); Minetuhan Spur: 1800–2100 m, *Clemens 33864* (BM); Mount Kinabalu: 3400 m, *Haviland 1092* (BM, K, L, SING), 3000 m, *Low s.n.* (K), 3400 m, *Native Collector 39* (K), 2700 m, *Nicholson SAN 17823* (K, SING), *Rao et al. 76* (SING), 3100 m, *Rickards 161* (K); Mt. Tembuyuken: *Nais et al. SNP 4830* (SNP); Paka-paka Cave: 3100 m, *Carr SFN 27632* (SING), *Clemens 10565* (K), 3400 m, *27930* (BM, L), 3000 m, *29328* (BM, K, L, SING), 3200 m, *30030* (K), 3000 m, *Gibbs 4238* (BM), 3100 m, *Holttum s.n.* (SING), 3000 m, *Meijer SAN 29271* (K, L), 2700 m, *Smythies S 10622* (K, L, SING), *Wyatt-Smith 80371* (K, L, SING); Paka-paka Cave/Panar Laban: 3200–3400 m, *Kokawa & Hotta 3451* (L), 3200–3400 m, *3497* (L); Paka-paka Cave/Summit Area: 2700–3700 m, *Gibbs 4273* (BM, K); Panar Laban: 3500 m, *Beaman 8297* (MSC), 3400 m, *Nais & Dolois SNP 3277* (SNP), 3300 m, *Smith 474* (L), 3400 m, *Stone 11348* (L), 3400 m, *11373* (L); Park Headquarters: 1200 m, *Meijer SAN 22114* (K), 1700 m, *de Laubenfels P 645* (L); Park Headquarters/Power Station: 1600 m, *Cockburn & Aban SAN 82973* (K, L); Pig Hill: 2000–2300 m, *Beaman 9843* (MSC); Sayat-sayat: 3500 m, *Carr SFN 27617* (BM, SING); Sheila's Plateau: 3400 m, *Fuchs & Collenette 21430* (K); Summit Area: 3600 m, *Anderson S 27089* (K), 3600 m, *S 27090* (L), 3400–4000 m, *Kokawa & Hotta 3563* (L); Summit Trail: 3100 m, *de Laubenfels P 636* (L).

33. Podocarpaceae

De Laubenfels, D. J. Podocarpaceae. Fl. Males. I, 10: 351–419. 1988.

33.1. Dacrycarpus

De Laubenfels, D. J. *Dacrycarpus*. Fl. Males. I, 10: 374–384. 1988. De Laubenfels, D. J. A revision of the Malesian and Pacific rainforest conifers, I. Podocarpaceae, in part. J. Arnold Arb. 50: 315–337. 1969.

33.1.1. Dacrycarpus imbricatus (Blume) de Laub.

33.1.1a. Dacrycarpus imbricatus var. **patulus** de Laub., J. Arnold Arb. 50: 320. 1969. Fig. 6.

Large tree. Lower montane forest. Elevation: 1400–2400 m.

Specimens Examined. Gurulau Spur: 1700 m, *Clemens 50696* (BM), 2300 m, *51024* (BM); Kadamaian River: 2000 m, *Carr SFN 27735* (SING); Kemburongoh: 2000 m, *Carr SFN 27553* (BM, SING), 1500 m, *Clemens 28954* (K), 1500 m, *Fosberg 44128* (K, L); Kiau View Trail: *Aban SAN 56305* (SING); Kinateki River Head: 2400 m, *Clemens 35011* (BM); Kundasang: *Burgess SAN 25162* (SING); Liwagu River Trail: 1500 m, *Sadau SAN 42811* (SNP); Mamut Hill: 1400–1700 m, *Kokawa & Hotta 5384* (L); Mamut/Bambangan River: 1400–1700 m, *Kokawa & Hotta 5514* (L); Mesilau Cave Trail: 1700–1900 m, *Beaman 8008* (MSC); Mesilau River: 1500 m, *RSNB 4084* (K, L, SING), *Clemens 51635* (BM, K, L); Mount Kinabalu: *Lajangah SAN 33085* (K, L, SING); Park Headquarters: *Abbe et al. 9994* (SING), *Tan & Gimpiton SNP 507* (SNP), 1600 m, *Thomas & Patrick SNP 235* (SNP); Park Headquarters/Power Station: 1600 m, *Cockburn & Aban SAN 82961* (K, L), 1700–1900 m, *Kokawa & Hotta 3217* (L), 1600 m, *Mikil SAN 33930* (SNP); Penataran Basin: 2400 m, *Clemens 33618* (BM, K, L); Pinosuk Plateau: *Chow & Leopold SAN 74521* (K, L, SING), 1500 m, *Sadau SAN 42890* (K, L); Sosopodon: 1500 m, *Sario SAN 32246* (K); Tenompok: 1500 m, *Clemens 28631* (BM, K, L, SING), 1500 m, *29779* (BM, K, L), 1400 m, *Melegrito A 471* (K, L, SING), 1400 m, *Smythies S 10601* (K, L, SING); Tenompok/Ranau: 1500 m, *Carr SFN 27010* (SING).

33.1.2. Dacrycarpus kinabaluensis (Wasscher) de Laub., J. Arnold Arb. 50: 330. 1969. Fig. 7.

Podocarpus cupressina Stapf, non R. Br. ex Mirbel, Trans. Linn. Soc. Bot. 4: 249. 1894.

Podocarpus imbricatus Blume var. *kinabaluensis* Wasscher, Blumea 4: 400. 1941.—Type: Above Paka-paka Cave, 3900 m, *Clemens 27854* (holotype: B†; isotype: BM!).

Shrub, treelet, or small tree, frequently gnarled. Upper montane forest, especially on ultramafic substrate, extending to upper limit of scrub vegetation. Elevation: 2100–4000 m. Endemic to Mount Kinabalu.

Additional Specimens Examined. Eastern Shoulder: 3200 m, *RSNB 868* (K, L, SING), *Phillipps et al. SNP 2388* (SNP); Gurulau Spur: 3000 m, *Clemens 51066* (BM), 3400 m, *51201* (BM, L); Janet's Halt: 2400 m, *Collenette 579* (K); Layang-layang/Panar Laban: 2700–3400 m, *Kokawa & Hotta 3380* (L); Lubang/Granite Cap: *Gibbs 4216* (K); Marai Parai: 3000–3400 m, *Clemens 32316* (K, L), 3000–3400 m, *32316A* (BM), 3400 m, *32317* (BM, L), 3400 m, *32318* (BM, L); Marai Parai Spur: *Gibbs 4216* (BM); Mesilau Front: 2700–3400 m, *RSNB 5887* (K, L); Mount Kinabalu: *Binideh SAN 65173* (K), 3100 m, *Cockburn SAN 82988* (K), 3200 m, *Cockburn & Aban SAN 82972* (K), 3200 m, *SAN 82978* (K, L), 3200 m, *SAN 82981* (K), 3400 m, *Haviland 1094* (K, SING), 3400 m, *1095* (K, SING), 3000 m, *Nicholson SAN 17825* (K, SING), 2700 m, *SAN 39766* (K, L, SING), 2100 m, *Rao et al. 83* (SING); Paka-paka Cave: 3100 m, *Carr SFN 28052* (SING), 3400 m, *Clemens 28910* (K, L), 3100 m, *Holttum s.n.* (SING), 3000 m, *Meijer SAN 21988* (K), 3000 m, *SAN 29265* (K, L), 3300 m, *Sinclair et al. 9146* (K, SING), 3200 m, *Wood & Wyatt-Smith SAN 4493* (SING); Paka-paka Cave/Panar Laban: 3200 m, *Wood & Wyatt-Smith SAN 4493* (L); Panar Laban: 3500 m, *Anonymous SNP 2337* (SNP), 3400 m, *Boeriaatmadja 89* (L), *Justine SNP 676* (SNP), 3400 m, *Phillipps & Tan SNP 1594* (SNP), 3300 m, *Smith 471* (L), 3400 m, *Stone 11368* (L); Panar Laban/Sayat-sayat: 3400–3700 m, *Sato UKMS 764* (SNP); Sayat-sayat: 3800 m, *Cockburn & Aban SAN 82771* (K, L); Summit Area: 3400 m, *Anderson S 27079* (K), 4000 m, *Clemens 27092* (BM, K, L), 3800 m, *29914* (K, L), 3700 m, *Kokawa & Hotta 3640* (L), 3600 m, *3642* (L); Summit Trail: 2800–3000 m, *Beaman SNP 5062* (SNP), 3000 m, *8305* (K, MSC), *Clemens 10636* (K), 3600 m, *Jacobs 5755* (K, L), 2800 m, *de Laubenfels P 631* (L), 2800 m, *P 632* (L), 3100 m, *P 635* (L).

33.2. Dacrydium

De Laubenfels, D. J. *Dacrydium*. Fl. Males. I, 10: 360–371. 1988. De Laubenfels, D. J. A revision of the Malesian and Pacific rainforest conifers, I. Podocarpaceae, in part. J. Arnold Arb. 50: 282–308. 1969.

33.2.1. Dacrydium beccarii Parl. in DC., Prodr. 16, 2: 494. 1868. Fig. 8.

Shrub or small tree. Lower montane forest, probably on ultramafic substrate. Elevation: 1500–1600 m. This record may be questionable, but the specimen cited was determined by de Laubenfels.

Specimen Examined. Mamut Hill: 1500–1600 m, *Kokawa & Hotta 6051* (L).

33.2.2. Dacrydium gibbsiae Stapf in Gibbs, J. Linn. Soc. Bot. 42: 192. 1914.—Type: Lubang/Granite Core, 1800–3700 m, *Gibbs 4162* (holotype: BM!; isotype K!). Fig. 9.

Dacrydium beccarii Parl. in DC. var. *kinabaluense* Corner, Gardens' Bull. 10: 244, t. 9. 1939.—Type: Penibukan, 1400 m, *Carr SFN 26437* (holotype: SING!).

Shrub or small tree with pendulous branches. Upper montane forest on ridges, rarely lower montane forest, often on ultramafic substrate. Elevation: 1400–3700 m. Endemic to Mount Kinabalu.

ADDITIONAL SPECIMENS EXAMINED. KEMBURONGOH/PAKA-PAKA CAVE: 2700–3400 m, *Clemens s.n.* (BM); LAYANG-LAYANG: 2700–2900 m, *Hotta 3897* (L), 2700–2900 m, *3900* (L); LAYANG-LAYANG/PAKA-PAKA CAVE: 2700–3200 m, *Kokawa & Hotta 3401* (L); LUBANG/PAKA-PAKA CAVE: *Clemens 10685* (BM, K); MARAI PARAI: 1600 m, *Argent SNP 2379* (SNP), 1600 m, *Carr SFN 26588* (SING), 1500–1800 m, *Clemens 33037* (BM, L), 1500 m, *Collenette A 100* (BM); MARAI PARAI SPUR: 1500–2400 m, *Gibbs 4050* (BM), 1800 m, *Phillipps SNP 1821* (SNP); MOUNT KINABALU: 2400 m, *Low s.n.* (K), 2600 m, *Meijer SAN 22045* (K, SING), 2700 m, *Nicholson SAN 17826* (L, SING), 2900–3300 m, *Rickards 153* (K), 2400 m, *Whitehead s.n.* (BM); PAKA-PAKA CAVE: 2100–2700 m, *Enriquez SFN 18168* (SING); PENATARAN BASIN: 2000 m, *Clemens 40151* (BM); PENIBUKAN: 1500 m, *Clemens 30922* (BM, L); PIG HILL: 2100 m, *RSNB 4361* (K, L, SING); PINOSUK PLATEAU: 1600 m, *Collenette 542* (K); SUMMIT TRAIL: 2800–3000 m, *Beaman SNP 5063* (SNP), 3000 m, *8306* (K, MSC), 2800 m, *de Laubenfels P 628* (L), 2800 m, *P 629* (L), 2200 m, *P 630* (L).

33.2.3. Dacrydium gracilis de Laub., Fl. Males. I, 10(3): 367. 1988.—TYPE: Park Headquarters, 1500 m, *de Laubenfels P 716* (holotype: L!). Fig. 10.

Large tree. Lower montane forest. Elevation: 1400–1600 m.

ADDITIONAL SPECIMENS EXAMINED. HEMPUEN HILL: 1400 m, *Beaman et al. SNP 5070* (SNP); LETENG TRAIL: 1500 m, *Meijer SAN 21086* (K, SING), 1500 m, *SAN 21098* (K, SING), 1500 m, *SAN 21100* (K, SING); LIWAGU RIVER TRAIL: 1500 m, *de Laubenfels P 638* (L), 1500 m, *P 642* (L); MESILAU RIVER: 1500 m, *RSNB 4303* (K, SING), 1500 m, *RSNB 4305* (K, SING); PARK HEADQUARTERS: 1500 m, *de Laubenfels P 717* (L); PARK HEADQUARTERS/POWER STATION: 1600 m, *Cockburn SAN 82963* (K), 1600 m, *SAN 82965* (K), 1600 m, *Cockburn & Aban SAN 82959* (K), 1600 m, *SAN 82962* (K); TENOMPOK: 1600 m, *Mujin SAN 33774* (K, L).

33.2.4. Dacrydium pectinatum de Laub., J. Arnold Arb. 50: 289. 1969. Fig. 11.

Medium-sized tree (on Mount Kinabalu). Hill forest on ultramafic substrate. Elevation: 800–1600 m.

SPECIMENS EXAMINED. HEMPUEN HILL: 800 m, *Abbe et al. 9938* (L), 800 m, *9939* (SING), 1100 m, *9952* (L), 1400 m, *Beaman et al. SNP 5071* (SNP), 900–1200 m, *Meijer SAN 20951* (L), 1200 m, *SAN 20952* (L), 1300 m, *SAN 20970* (K, SING); KIAU VIEW TRAIL: 1600 m, *Justine SNP 290* (SNP).

33.2.5. Dacrydium xanthandrum Pilger, Bot. Jahrb. 69: 252. 1938. Fig. 12.

Small to medium-sized tree. Lower montane forest, upper montane forest, especially in mossy forest on ridges. Elevation: 1400–3000 m.

SPECIMENS EXAMINED. JANET'S HALT: 2400 m, *Collenette 543* (K), 2400 m, *Nicholson SAN 39768* (K); KEMBURONGOH: 2100 m, *Anonymous SAN 62031* (K), 2100 m, *Meijer SAN 29153* (K, L), 2100 m, *Price 205* (K), 1800 m, *Smythies S 10607* (K, SING); KILEMBUN RIVER HEAD: 1800 m, *Clemens 32502* (BM, K, L); KUNDASANG: 1800 m, *Meijer SAN 23500* (K, SING); LETENG TRAIL: 1700 m, *Meijer SAN 21097* (K, SING); MAMUT/BAMBANGAN RIVERS: 1400–1700 m, *Kokawa & Hotta 5565* (L); MESILAU HILL: 2300 m, *RSNB 8024* (K, L); MOUNT KINABALU: 1800–2100 m, *Enriquez 18169* (SING), 2000 m, *Haviland 1183* (K, SING), 2700 m, *Holttum s.n.* (SING), 2700 m, *Nicholson SAN 17827* (K, SING); MURU-TURA RIDGE: 1500–1800 m, *Clemens 34341* (BM, K, L); PAKA-PAKA CAVE: 2400–3000 m, *Clemens 28542* (BM); SUMMIT TRAIL: 2100 m, *Aban SAN 62031* (L), 2100–2300 m, *Beaman & Beaman SNP 5061* (SNP), 2700 m, *Carr SFN 27599* (SING), 2000 m, *Cockburn & Aban SAN 82971* (K), 1800 m, *Smythies S 10607* (L), 2700 m, *de Laubenfels P 626* (L), 2700 m, *P 627* (L).

33.3. Falcatifolium

De Laubenfels, D. J. *Falcatifolium*. Fl. Males. I, 10: 371–374. 1988. De Laubenfels, D. J. A revision of the Malesian and Pacific rainforest conifers, I. Podocarpaceae, in part. J. Arnold Arb. 50: 308–314. 1969.

33.3.1. Falcatifolium falciforme (Parl.) de Laub., J. Arnold Arb. 50: 309. 1969. Fig. 13.

Podocarpus falciformis Parl. in DC., Prodr. 16, 2: 685. 1868.
Dacrydium falciforme (Parl.) Pilger, Pflanzenr. IV, 5, Heft 18: 45. 1903.

Small to medium-sized tree. Hill forest, lower montane forest, sometimes on ultramafic substrate. Elevation: 800–2100 m.

Specimens Examined. Hempuen Hill: *Abbe et al. 9940* (SING), 800–1200 m, *Beaman 7668* (MSC), 1400 m, *Beaman et al. SNP 5075* (SNP), 1300 m, *Madani SAN 89369* (K), 1200–1400 m, *Meijer SAN 20279* (L, SING), 1200 m, *SAN 20953* (K), 1500 m, *de Laubenfels P 707* (L); Kemburongoh: 2100 m, *Clemens 27851* (BM, K); Liwagu River Trail: 1500 m, *de Laubenfels P 639* (L), 1500 m, *P 640* (L); Lumu-lumu: 1600 m, *Carr SFN 27241* (SING); Marai Parai: *Argent & Phillipps SNP 2732* (SNP), 1500 m, *Clemens 33078* (K, L), 1500 m, *Holttum s.n.* (SING), *Phillipps SNP 1145* (SNP), *SNP 2762* (SNP); Marai Parai Spur: *Clemens 10962* (K), 1500 m, *Holttum s.n.* (SING); Marai Parai Spur/Dapatan & Penibukan Ridges: 1500 m, *Gibbs 4067* (K); Mesilau River: 1500 m, *RSNB 4847* (K, L, SING); Park Headquarters: 1600 m, *Patrick & Gimpiton SNP 499* (SNP), 1600 m, *Tan & Gimpiton SNP 568* (SNP), 1500 m, *de Laubenfels P 718* (L), 1500 m, *P 719* (L); Park Headquarters/Power Station: 1600 m, *Cockburn SAN 82966* (K, L), 1700–1900 m, *Kokawa & Hotta 3213* (L); Penibukan: 1200–1500 m, *Clemens s.n.* (BM, K, L); Pinosuk Plateau: 1700 m, *RSNB 1863* (K, L, SING).

33.4. Nageia

De Laubenfels, D. J. *Nageia*. Fl. Males. I, 10: 389–395. 1988. De Laubenfels, D. J. Revision of the genus *Nageia* (Podocarpaceae). Blumea 32: 209–211. 1987. De Laubenfels, D. J. A revision of the Malesian and Pacific rainforest conifers, I. Podocarpaceae, in part [*Nageia* as *Decussocarpus*]. J. Arnold Arb. 50: 340–359. 1969. Fu, D. Z. 1992. Nageiaceae—a new gymnosperm family. Acta Phytotax. Sin. 30: 515–528.

33.4.1. Nageia wallichiana (Presl) Kuntze, Rev. Gen. Pl. 2: 800. 1891. Fig. 14.

Medium-sized to large tree. Lower montane forest. Elevation: 1500 m.

Specimens Examined. Mesilau River: 1500 m, *RSNB 4878* (K, L, SING), 1500 m, *de Laubenfels P 624* (L); Penibukan: *Clemens s.n.* (BM); Sosopodon: *Aban SAN 62022* (K, SING).

33.5. Podocarpus

De Laubenfels, D. J. *Podocarpus*. Fl. Males. I, 10: 395–419. 1988. De Laubenfels, D. J. A taxonomic revision of the genus *Podocarpus*. Blumea 30: 251–278. 1985. Wasscher, J. The genus *Podocarpus* in the Netherlands Indies. Blumea 4: 359–542. 1941. Gray, N. E. A taxonomic revision of *Podocarpus*, XI. The South Pacific species of section *Podocarpus*, subsection B. J. Arnold Arb. 39: 424–477. 1958.

33.5.1. Podocarpus brevifolius (Stapf) Foxw., Philipp. J. Sci., Bot. 6: 160, t. 29. 1911. Fig. 15.

Podocarpus neriifolius D. Don in Lambert var. *brevifolius* Stapf, Trans. Linn. Soc. Bot. 4: 249. 1894.—Type: Mount Kinabalu, 3400 m, *Haviland 1093* (syntype: K!), 3700 m, *Low s.n.* (syntype: K!).

Small tree or shrub, often gnarled. Mostly upper montane forest, rarely lower montane forest, on ultramafic substrate or in granitic crevices. Elevation: 1200–3800 m. Endemic to Mount Kinabalu.

Additional Specimens Examined. Eastern Shoulder: 3000 m, *RSNB 724* (K, L, SING), 3000 m, *RSNB 756* (K, L, SING), 2400 m, *Collenette 810* (K, L, SING); Gurulau Spur: 2100–2700 m, *Clemens 50790* (BM), 3400–3700 m, *50825* (BM, L); Layang-layang/Paka-paka Cave: 2700–3200 m, *Kokawa & Hotta 3411* (L); Layang-layang/Panar Laban: 2700–3400 m, *Kokawa & Hotta 3379* (L); Lubang/Granite Core: 1800–3700 m, *Gibbs 4166* (BM); Mamut Copper Mine: 1400–1500 m, *Beaman 10362* (K, MSC); Marai Parai Spur: 1500–2400 m, *Gibbs 4089* (BM, K); Mesilau River: 3500 m, *Smith 529* (L); Mount Kinabalu: 2700–3000 m, *Meijer SAN 22065* (K, SING), 3000 m, *Nicholson SAN 17824* (K, SING), 3400 m, *Rao et al. 77* (SING); Mt. Tembuyuken: *Nais et al. SNP 4834* (SNP); Paka-paka Cave: 3400 m, *Clemens 27103* (BM), 3400 m, *28901* (K, L), 3100 m, *Holttum s.n.* (SING), 3400 m, *Lampangi SAN 29290* (K, L, SING); Panar Laban: 3500 m, *Anonymous SNP 2335* (SNP), *Cockburn SAN 82780* (K, L), 3400 m, *Cockburn & Aban SAN 82276* (K), 3400 m, *SAN 82776* (L), 3400 m, *Phillipps & Tan SNP 1586* (SNP), 3400 m, *Stone 11351* (L), 3400–3700 m, *Wong 21* (SING); Penibukan: 1200 m, *Clemens s.n.* (BM, K); Summit Area: 3400 m, *Anderson S 27094* (K), 3800 m, *Clemens 27826* (BM); Summit Trail: 2800–3000 m, *Beaman SNP 5064* (SNP), *Clemens 10657* (K), 3600 m, *Lee et al. SAN 69959* (SNP), 2700 m, *Meijer SAN 21975* (K), 3000 m, *de Laubenfels P 633* (L), 3100 m, *P 634* (L); Upper Kinabalu: 3800 m, *Clemens 27825* (K, L).

33.5.2. Podocarpus confertus de Laub., Blumea 30: 271. 1985. Fig. 16.

Small to large tree. Hill forest on ultramafic substrate. Elevation: 600–1200 m.

Specimens Examined. Hempuen Hill: *Aban SAN 90606* (K, L), 600 m, *Madani SAN 89400* (K, L), 1200 m, *de Laubenfels P 712* (L), 1200 m, *P 713* (L), 1200 m, *P 714* (L).

33.5.3. Podocarpus gibbsii N. E. Gray, J. Arnold Arb. 39: 429. 1958.—Type: Marai Parai, 1500 m, *Clemens 32021* (holotype: A, n.v.; isotypes BM! K! L!). Fig. 17.

Small to medium-sized tree. Lower montane forest, upper montane forest, mossy ridge forest, on ultramafic substrate. Elevation: 1200–2400 m. Endemic to Mount Kinabalu.

Additional Specimens Examined. Hempuen Hill: 1500 m, *de Laubenfels P 709* (L), 1500 m, *P 710* (L), 1500 m, *P 711* (L); Kilembun Basin: 1500 m, *Clemens 40001* (BM, K, L); Marai Parai: *Phillipps SNP 2761* (SNP); Marai Parai Spur/Penibukan: 1500–2400 m, *Gibbs 4092* (BM, K); Penibukan: 1400 m, *Carr SFN 26450* (SING), 1200–1500 m, *Clemens s.n.* (L); Pig Hill: 2100 m, *RSNB 4369* (K, L, SING).

33.5.4. Podocarpus globulus de Laub., Blumea 30: 269. 1985. Fig. 18.

Small to medium-sized tree. Lower montane forest on ultramafic substrate. Elevation: 1500 m.

SPECIMENS EXAMINED. HEMPUEN HILL: 1500 m, *de Laubenfels P 704* (L), 1500 m, *P 705* (L), 1500 m, *P 706* (L).

33.5.5. Podocarpus laubenfelsii Tiong, Blumea 29: 523. 1984.—TYPE: Park Headquarters, 1500 m, *de Laubenfels P 715* (holotype: L!). Fig. 19.

Small to medium-sized tree. Lower montane forest. Elevation: 1400–1600 m.

ADDITIONAL SPECIMENS EXAMINED. LIWAGU/MESILAU RIVERS: 1400 m, *RSNB 2657* (K, L, SING); MESILAU RIVER: 1500 m, *RSNB 4350* (K, L, SING); PARK HEADQUARTERS: 1600 m, *Aban SAN 49409* (K), 1500 m, *de Laubenfels P 643* (L); SOSOPODON: 1500 m, *Gintus SAN 56374* (K, L).

33.5.6. Podocarpus neriifolius D. Don in Lambert, Gen. Pinus ed. 1: 21. 1824. Fig. 20.

Medium-sized to large tree. Lower montane forest. Elevation: 1100–1700 m.

SPECIMENS EXAMINED. GURULAU SPUR: 1700 m, *Clemens 50691* (BM, K, L); HEMPUEN HILL: 1400 m, *Beaman et al. SNP 5069* (SNP); MESILAU RIVER: 1500 m, *RSNB 4255* (K, L, SING); PENIBUKAN: 1100 m, *Clemens 50051* (BM, K, L).

33.6. Sundacarpus.

De Laubenfels, D. F. *Prumnopitys*. Fl. Males. I, 10: 384–389. 1988.

33.6.1. Sundacarpus amara (Blume) C. N. Page, Notes Roy. Bot. Gard. Edinburgh 45: 378. 1988. Fig. 21.

Prumnopitys amara (Blume) de Laub., Blumea 24: 190. 1978.

Large tree. Lower montane forest. Elevation: 1400–1700 m.

SPECIMENS EXAMINED. KINASARABAN HILL: 1400 m, *Badak SAN 32333* (L); MAMUT/BAMBANGAN RIVERS: 1400–1700 m, *Kokawa & Hotta 5541* (L); MESILAU CAMP: *RSNB 5858* (K, L); MESILAU RIVER: 1500 m, *RSNB 4211* (K, L, SING), 1500 m, *RSNB 7031* (K, L, SING), 1500 m, *RSNB 7102* (K, L, SING), 1500 m, *de Laubenfels P 622* (L), 1500 m, *P 623* (L); PARK HEADQUARTERS/POWER STATION: 1600 m, *Cockburn & Aban SAN 82967* (K, L); PINOSUK PLATEAU: 1500 m, *Sadau SAN 49689* (L); TENOMPOK: 1400 m, *Smythies S 10614* (K, L, SING), 1500 m, *Wood & Wyatt-Smith SAN 4500* (L, SING); TENOMPOK/KUNDASANG: 1500 m, *Meijer SAN 20411* (L).

34. GNETACEAE

Markgraf, F. Monographie der Gattung *Gnetum*. Bull. Jard. Bot. Buit., ser. 3, 10: 407–511. 1930. Markgraf, F. Gnetaceae. Fl. Males. I, 4(3): 336–347. 1951. Markgraf, F. Gnetaceae. (Addenda, corrigenda et emendanda). Fl. Males. I, 6: 944–949. 1972.

34.1. Gnetum

34.1.1. Gnetum cuspidatum Blume, Rumphia 4: 5. 1848. Fig. 22.

Woody climber. Lower montane forest. Elevation: 400–1700 m.

SPECIMENS EXAMINED. KAUNG: 400 m, *Carr SFN 27293* (SING); KILEMBUN BASIN: 1700 m, *Clemens 33671* (BM, L); TENOMPOK: 1400 m, *Clemens 26203* (BM, K, L), 1500 m, *26203b* (K, L).

34.1.2. Gnetum gnemonoides Brongn. in Duperrey, Voy. Coquille, 12. 1829. Fig. 23.

Woody climber with exceptionally large seeds (2.5–3 × 4.5–6 cm). Lowlands. Elevation: 600 m.

SPECIMENS EXAMINED. PINAWANTAI: 600 m, *Shea & Aban SAN 76917* (K, SING).

34.1.3. Gnetum klossii Merr. ex Markgraf, Bull. Jard. Bot. Buit., ser. 3, 10: 478, t. 11, f. 68. 1930. Figs. 24, 25.

Large woody climber. Hill forest. Elevation: 900 m.

SPECIMENS EXAMINED. DALLAS: 900 m, *Clemens 26003* (K, L), 900 m, *26003b* (K), 900 m, *27021* (K, L), 900 m, *27022* (BM).

34.1.4. Gnetum latifolium Blume, Tijd. Nat. Geschied. & Phys. 1: 160. 1834.

34.1.4a. Gnetum latifolium var. **latifolium.** Fig. 26.

Large woody climber. Lower montane forest. Elevation: 1200–1500 m.

SPECIMENS EXAMINED. BAMBANGAN RIVER: 1500 m, *RSNB 4629* (K, L, SING); MESILAU CAMP: 1300 m, *Meijer SAN 38567* (L); MESILAU RIVER: 1500 m, *RSNB 4229* (K, L, SING); PENIBUKAN: 1200–1500 m, *Clemens 30764* (K, L); SOSOPODON: *Sinanggul SAN 47907* (K, L).

34.1.4b. Gnetum latifolium var. **minus** (Foxw.) Markgraf, Bull. Jard. Bot. Buit., ser. 3, 10: 463. 1930. Fig. 27.

Woody climber. Hill forest, lower montane forest. Elevation: 900–1800 m.

SPECIMENS EXAMINED. DALLAS/BONGOL: 900 m, *Clemens 27645* (BM, L); GURULAU SPUR: 1500 m, *Clemens 50509* (BM, K, L); TENOMPOK: 1200 m, *Clemens 26826* (BM, L, SING), 1500 m, *27506* (BM, K), 1500 m, *27764* (BM, K, L); TINEKUK FALLS: 1800 m, *Clemens 40875* (BM, K, L).

34.1.5. Gnetum leptostachyum Blume, Rumphia 4: 5. 1848.

34.1.5a. Gnetum leptostachyum var. **leptostachyum.** Figs. 28, 29.

Woody climber. Hill forest, lower montane forest. Elevation: 600–1500 m.

SPECIMENS EXAMINED. DALLAS: 900 m, *Clemens s.n.* (BM), 900–1200 m, *26246* (BM, K, L), 900 m, *26264* (L), 900 m, *26284* (K), 900 m, *26429* (BM, K), 900 m, *26598* (K, L), 900 m, *26672* (BM, K, L), 900 m, *26698* (BM, K, L), 900 m, *26710* (BM, K, L), 900 m, *26848* (BM, K), 900 m, *27034* (K), 900 m, *27356* (L), 900 m, *27597* (K), 900 m, *27643* (BM, K), 900 m, *30311* (K, L); DALLAS/TENOMPOK: 1200 m, *Clemens 27597* (BM); GURULAU SPUR: 1500 m, *Clemens 51039* (BM, K, L); KAUNG: 800 m, *Mujin SAN 26759* (K, L); LIWAGU/MESILAU RIVERS: 1200 m, *RSNB 2595* (K, L, SING), 1200 m, *RSNB 2600* (K, L); LOHAN RIVER: 700–900 m, *Beaman 9242* (K, MSC); LOHAN/MAMUT COPPER MINE: 900 m, *Beaman 10640a* (K, MSC), 1000 m, *10645* (K, MSC); MARAI PARAI: 1500 m, *Clemens 33072* (BM, K, L); MINITINDOK GORGE: 900–1200 m, *Clemens 29670* (BM); MT. NUNGKEK: 900–1200 m, *Clemens 32728* (BM, L, SING); PORING

Hot Springs: 600 m, *Beaman 7545* (MSC); Poring Hot Springs/Langanan Water Falls: 600–1000 m, *Kokawa & Hotta 4904* (L); Singh's Plateau: 1000 m, *Meijer SAN 26418* (K, L, SING); Sosopodon: 1200 m, *Mikil SAN 37711* (K); Tenompok: *Clemens 27532* (BM, K, L), 1500 m, *29670* (K, L).

34.1.5b. Gnetum leptostachyum var. **abbreviatum** Markgraf, Reinwardtia 1: 462. 1952.—Type: Marai Parai, 1500 m, *Clemens 32990* (holotype: M?, n.v.; isotypes BM! L!). Fig. 30.

Woody climber. Lower montane forest, mostly on ultramafic substrate. Elevation: 1200–1800 m. Endemic to Mount Kinabalu.

Additional Specimens Examined. Kilembun River Head: 1800 m, *Clemens 32475* (BM, K, L); Lumu-lumu: 1600 m, *Carr SFN 27103* (SING); Marai Parai: 1500 m, *Clemens 32276* (BM, L), 1400 m, *32488* (BM, L), 1800 m, *32601* (L), 1200–1500 m, *32698* (L), 1500 m, *32991* (BM, K); Marai Parai Spur: 1800 m, *Clemens 32601* (BM); Marai Parai/Nungkek: 1200–1500 m, *Clemens 32698* (BM); Pinosuk Plateau: *Poore 1118* (K, L).

34.1.6. Gnetum neglectum Blume, Rumphia 4: 6, t. 175, f. 2. 1848. Fig. 31.

Woody climber. Hill forest. Elevation: 700–1100 m.

Specimens Examined. Eastern Shoulder: 1100 m, *RSNB 646* (K, SING); Hempuen Hill: *Beaman 7689* (MSC); Kipungit Hill: 700 m, *Beaman 7641* (K, MSC); Lohan River: 800–1000 m, *Beaman 9051* (K, MSC); Melangkap Kapa: 700–1000 m, *Beaman 8788* (K, MSC).

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Rickards 153 (33.2.2); 161 (32.1.1).
RSNB (lower than 2700) under Chew, Corner & Stainton; RSNB (higher than 4000) under Chew & Corner
Sadau 42811 (33.1.1a); 42812 (31.1.3); 42890 (33.1.1a); 49689 (33.6.1).
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Wong 21 (33.5.1).
Wood & Wyatt-Smith 4493 (33.1.2); 4500 (33.6.1).
Wyatt-Smith 80371 (32.1.1).

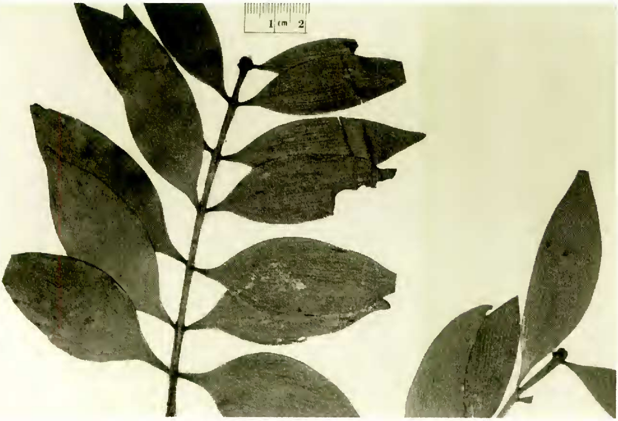

FIG. 2. *Agathis borneensis.* Leaves opposite, long-acuminate, parallel-veined; terminal bud globose. (*Beaman 7694,* K.)

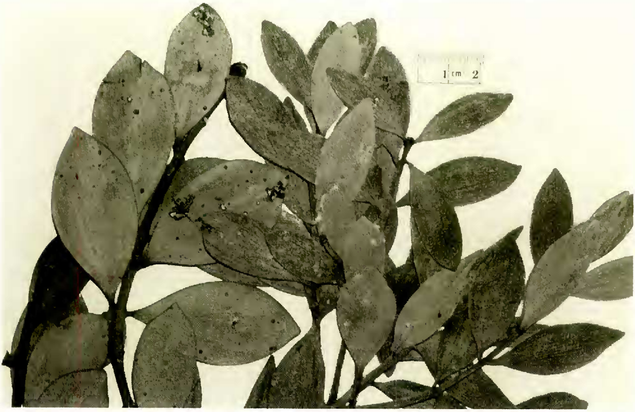

FIG. 3. *Agathis kinabaluensis.* Leaves opposite, short-acuminate, parallel-veined; terminal bud globose. (*Beaman 9556,* K.)

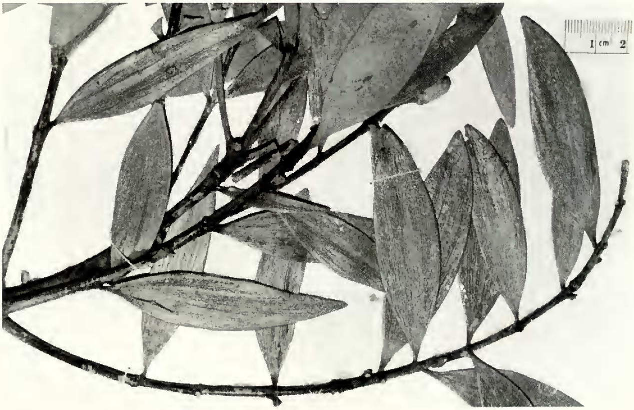

FIG. 4. *Agathis lenticulata.* Leaves opposite, hardly if at all acuminate, parallel-veined; terminal bud globose. (*Chew & Corner RSNB 4330,* K.)

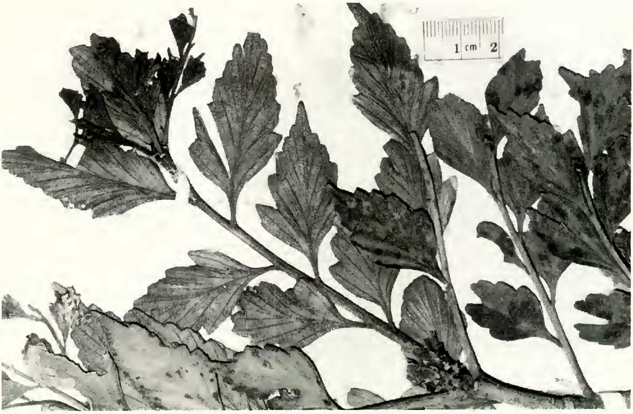

FIG. 5. *Phyllocladus hypophyllus.* True leaves absent on mature branches, these replaced by coarsely toothed, pinnately veined cladodes. (*Low s.n.* in 1851, holotype, K; one of the first specimens collected on Mount Kinabalu.)

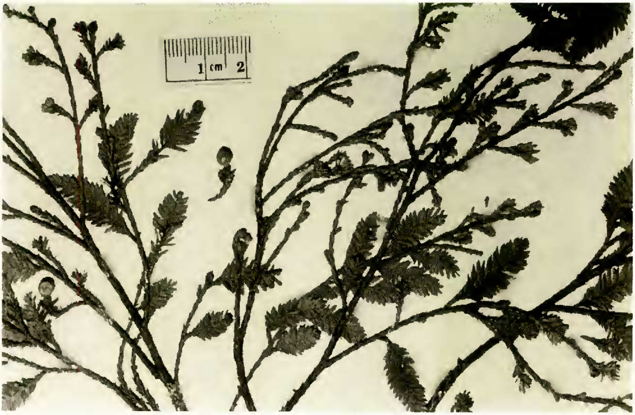

FIG. 6. *Dacrycarpus imbricatus* var. *patulus*. Leaves strongly dimorphic; juvenile leaves much larger, bilaterally flattened, distichous; adult leaves small, not bilaterally flattened, spirally arranged. (*Sadau SAN 42890*, K.)

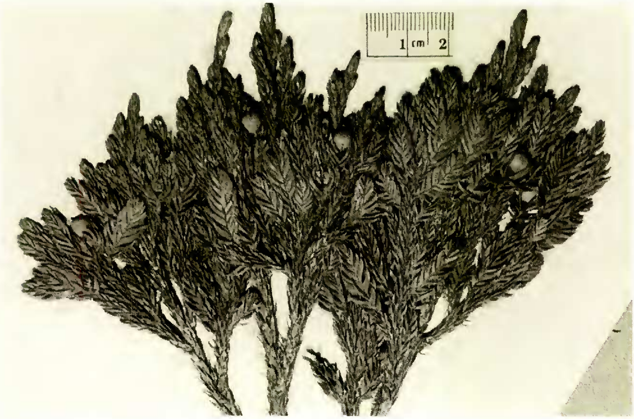

FIG. 7. *Dacrycarpus kinabaluensis*. Leaves dimorphic; juvenile leaves somewhat larger, bilaterally flattened, distichous; adult leaves somewhat smaller, not bilaterally flattened, spirally arranged. (*Chew & Corner RSNB 5887*, K.)

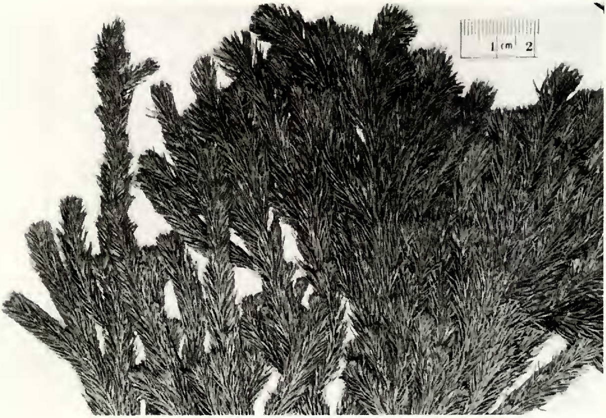

FIG. 8. *Dacrydium beccarii.* Leaves spirally arranged, relatively long, slender, straight, densely disposed on the stems, directed upward. (*Beccari 2385,* isotype, K; from Mt. Poe, Sarawak.)

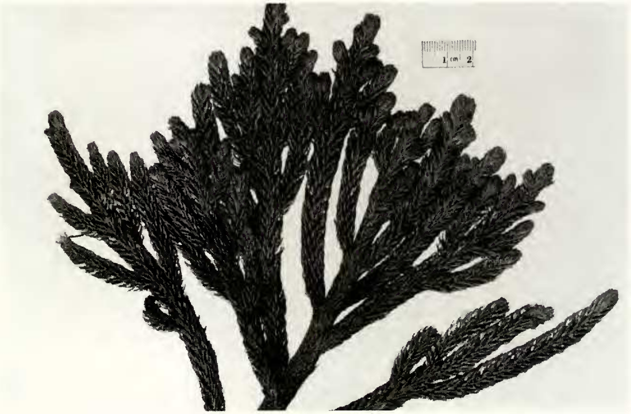

FIG. 9. *Dacrydium gibbsiae.* Leaves spirally arranged, the longest ca 1 cm long, thick and stiff, curved upward and inward. (*Beaman 8306,* K.)

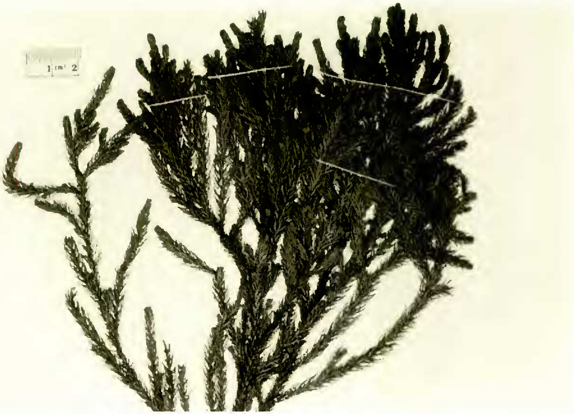

FIG. 10. *Dacrydium gracilis.* Leaves spirally arranged, the longest mature leaves mostly less than 1 cm long, relatively slender and straight, not extremely dense, directed upward but not stiffly curving inward. (*Cockburn & Aban SAN 82959,* K.)

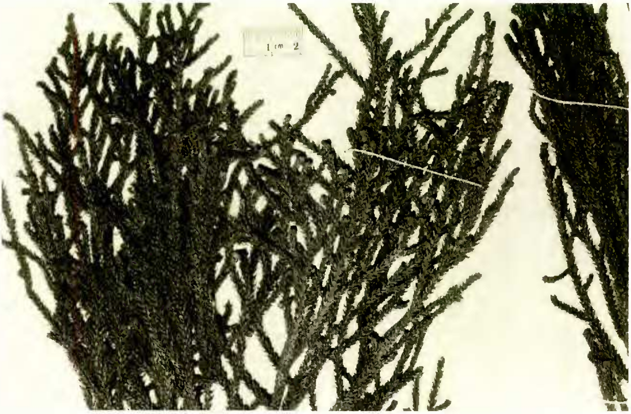

FIG. 11. *Dacrydium pectinatum.* Leaves spirally arranged, short and stiff, not more than 0.5 cm long on mature branches, directed upward and curving inward. (*Meijer SAN 20970,* K.)

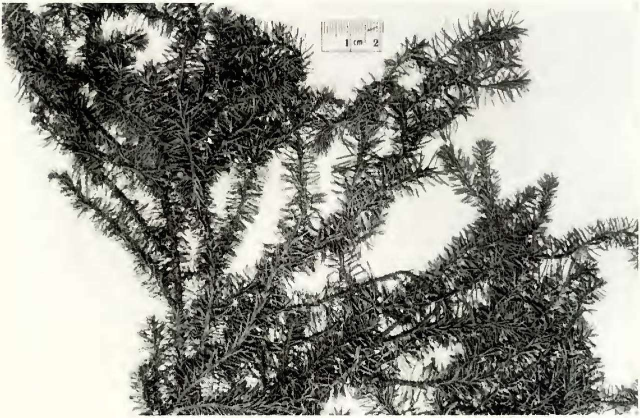

FIG. 12. *Dacrydium xanthandrum.* Leaves spirally arranged, relatively long and slender, ca 1 cm long, not very dense, mostly projecting perpendicular to the stem. (*Meijer SAN 23500,* K.)

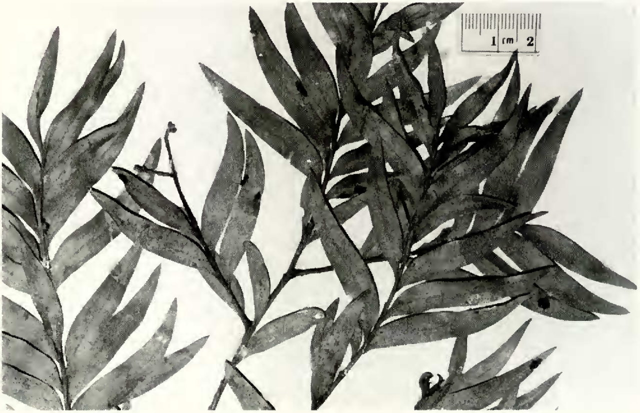

FIG. 13. *Falcatifolium falciforme.* Leaves spirally arranged but distichous, bilaterally flattened, single-veined, falcate, variable in size. (*Meijer SAN 20953,* K.)

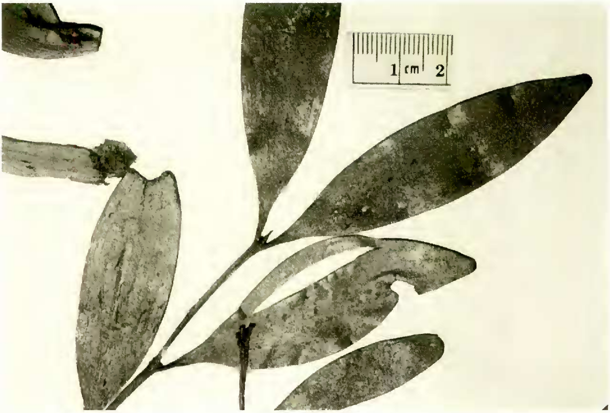

FIG. 14. *Nageia wallichiana.* Leaves opposite, elliptic, parallel-veined; terminal bud acuminate. (*Aban SAN 62022,* K.)

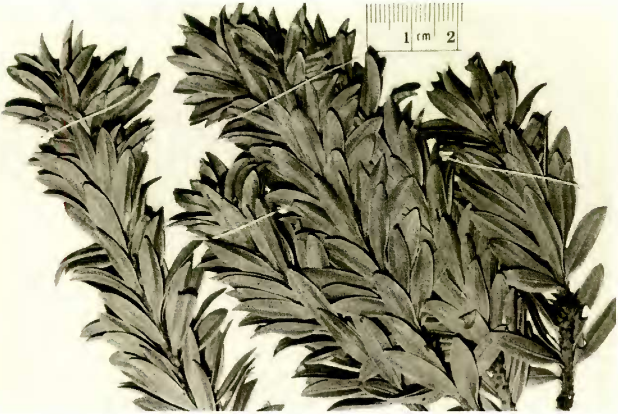

FIG. 15. *Podocarpus brevifolius.* Leaves spirally arranged, short, mostly 2–3 cm long, densely distributed on the stem, directed upward (in dried material), margin slightly revolute. (*Cockburn & Aban SAN 82276,* K.)

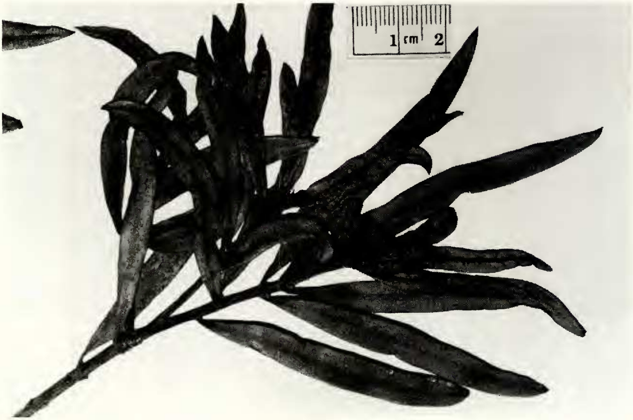

FIG. 16. *Podocarpus confertus.* Leaves spirally arranged or sometimes subopposite, long (ca 6–8 cm), relatively narrow, linear or linear lanceolate. (*Madani SAN 89400,* K.)

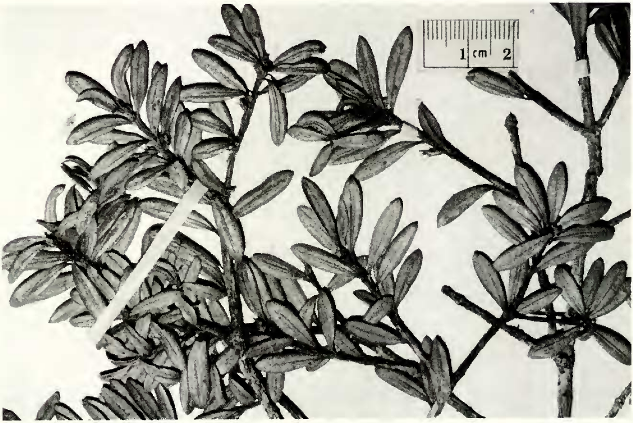

FIG. 17. *Podocarpus gibbsii.* Leaves spirally arranged, short, less than 2.5 cm long, oblanceolate, not appearing to be directed upward, margin revolute. (*Clemens 32021,* K, isotype.)

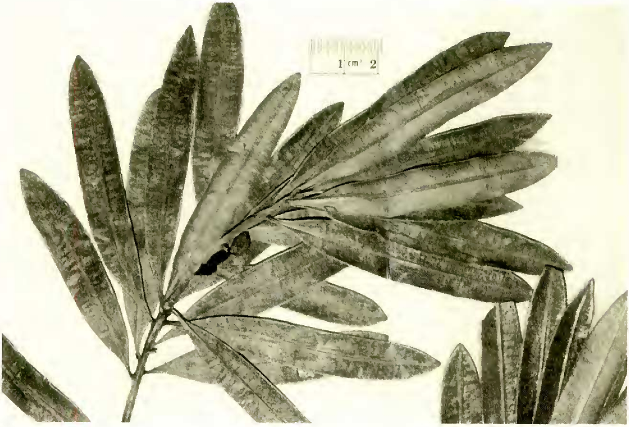

FIG. 18. *Podocarpus globulus.* Leaves spirally arranged or sometimes subopposite, relatively long (ca 7–8 cm), linear. (*De Laubenfels P688,* K, isotype; from Mt. Silam, Sabah.)

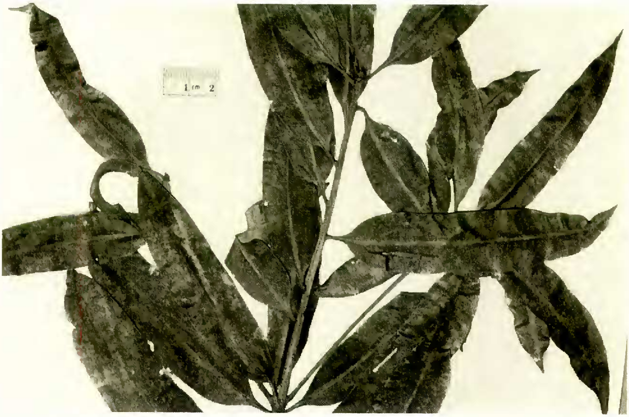

FIG. 19. *Podocarpus laubenfelsii.* Leaves spirally arranged, mostly linear-lanceolate, long (8–10 cm or more), unusually wide (sometimes 2 cm or more), acuminate. (*Chew et al. RSNB 2657,* K.)

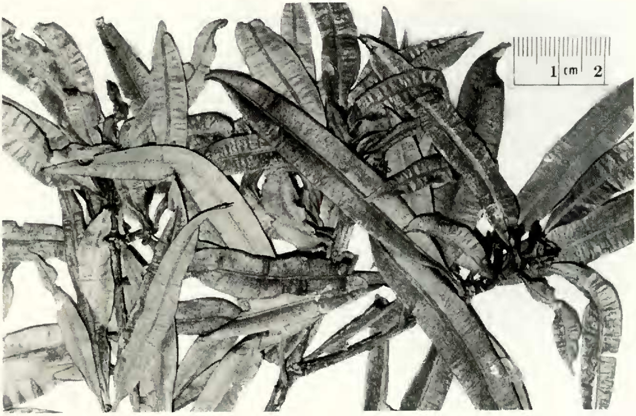

FIG. 20. *Podocarpus neriifolius.* Leaves spirally arranged, linear, long (often 8 cm or more), acuminate, the blade wrinkled perpendicular to midrib (especially in dried material). (*Chew & Corner RSNB 4255,* K.)

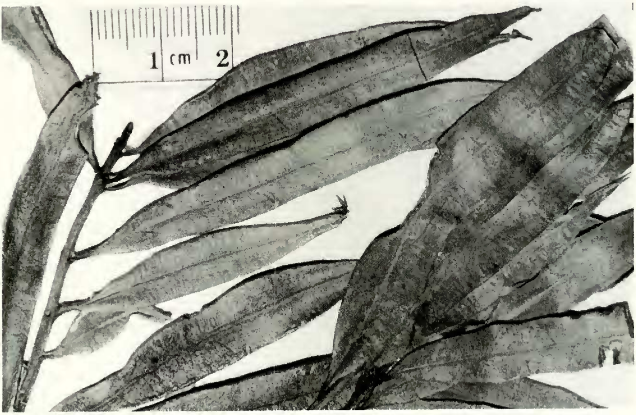

FIG. 21. *Sundacarpus amara.* Leaves spirally arranged, linear or linear-lanceolate, long-acuminate, midvein longitudinally grooved above. (*Cockburn & Aban SAN 82967,* K.)

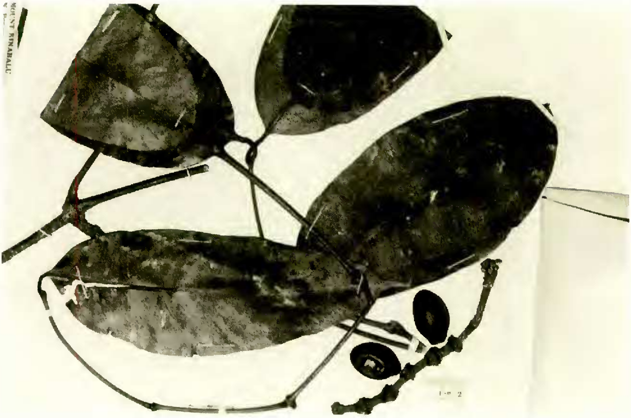

FIG. 22. *Gnetum cuspidatum.* Leaves opposite, acuminate, coriaceous; seeds sessile, less than 2.5 cm long, surface smooth, on short reproductive branches, borne from collars with thick hair masses. (*Clemens 26203,* K.)

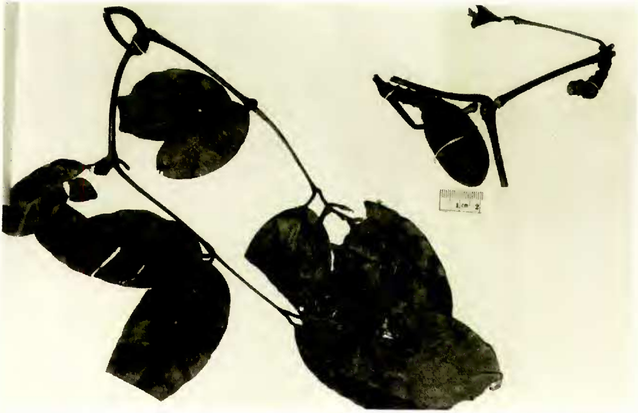

FIG. 23. *Gnetum gnemonoides.* Leaves opposite, ovate, acuminate; seeds 4.5–6 cm long. (*Shea & Aban SAN 76917,* K.)

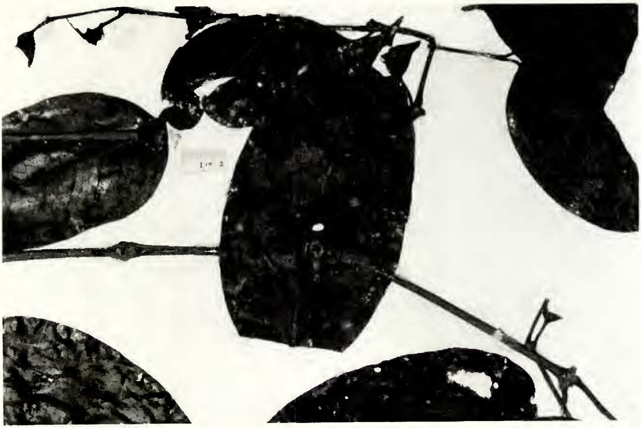

FIG. 24. *Gnetum klossii.* Leaves opposite, ovate-elliptic, acuminate, coriaceous. (*Clemens 26003,* K.)

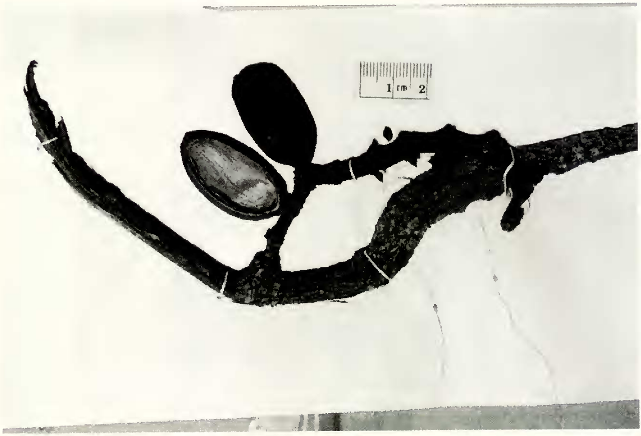

FIG. 25. *Gnetum klossii.* Seed surface roughened by wavy warts, brown; ♀ reproductive branches similarly roughened. (*Clemens 27021,* K.)

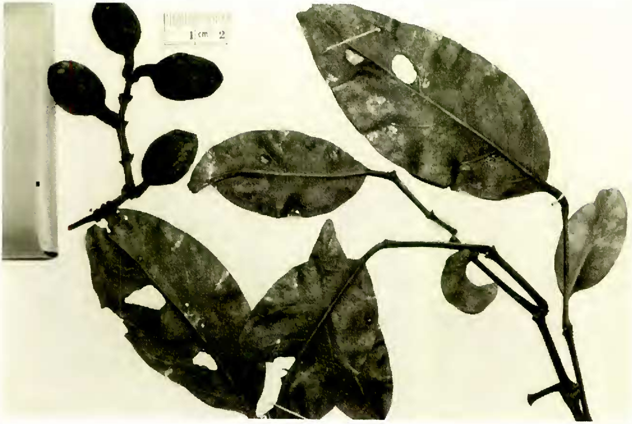

FIG. 26. *Gnetum latifolium* var. *latifolium*. Leaves opposite, ovate to narrowly ovate, coriaceous, mostly longer than 9 cm; seeds distinctly stalked, surface smooth (but wrinkled in dried material). (*Chew & Corner RSNB 4629*, K.)

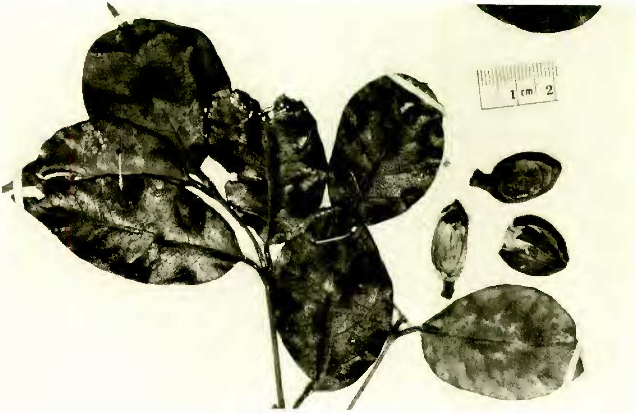

FIG. 27. *Gnetum latifolium* var. *minus*. Leaves opposite, elliptic, short-acuminate, coriaceous, short, not longer than 9 cm; seeds distinctly stalked, surface smooth (but wrinkled in dried material). (*Clemens 27506*, K.)

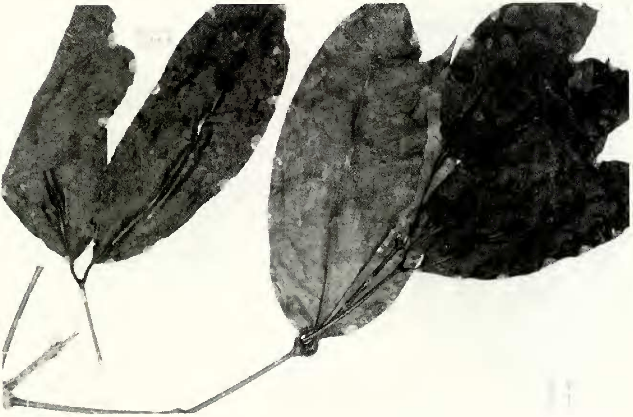

FIG. 28. *Gnetum leptostachyum* var. *leptostachyum*. Leaves opposite, elliptic-oblong, coriaceous, ca 20 cm or more long. (*Mujin SAN 26759*, K.)

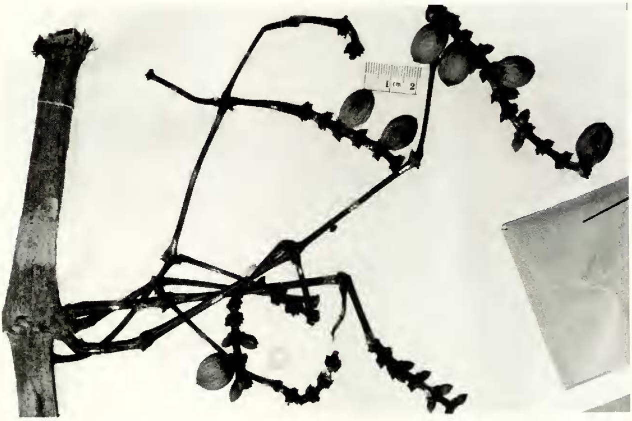

FIG. 29. *Gnetum leptostachyum* var. *leptostachyum*. Reproductive shoots several-branched; seeds sessile, surface smooth (but somewhat wrinkled in dried material). (*Mujin SAN 26759*, K.)

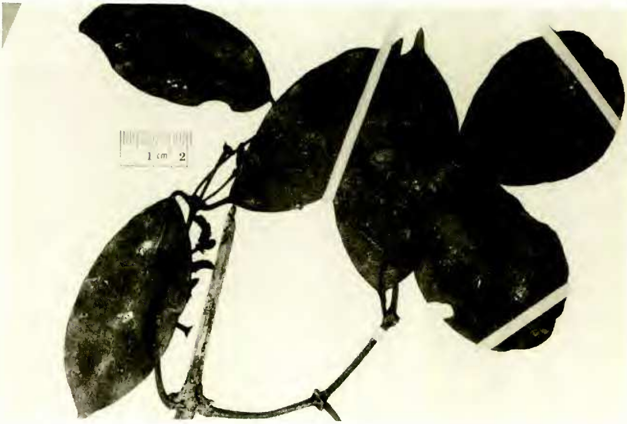

FIG. 30. *Gnetum leptostachyum* var. *abbreviatum*. Leaves opposite, elliptic-oblong, coriaceous, not more than 12 cm long. (*Clemens 32475*, K.)

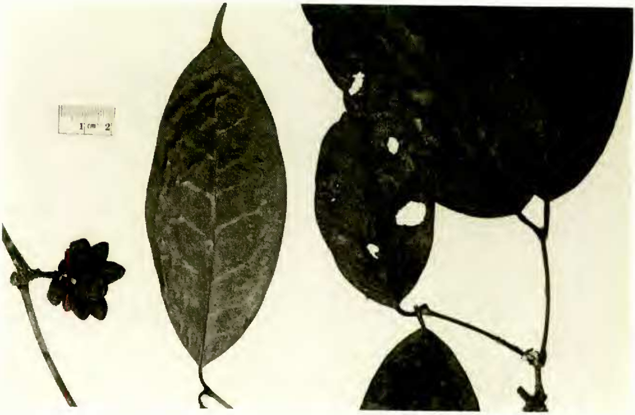

FIG. 31. *Gnetum neglectum*. Leaves opposite, lanceolate-elliptic or oblong, relatively thin. ♀ reproductive shoots short, unbranched or nearly so; seeds sessile, small, less than 2 cm long, surface smooth, borne from collars with thick hair masses. (*Beaman 7641*, K.)